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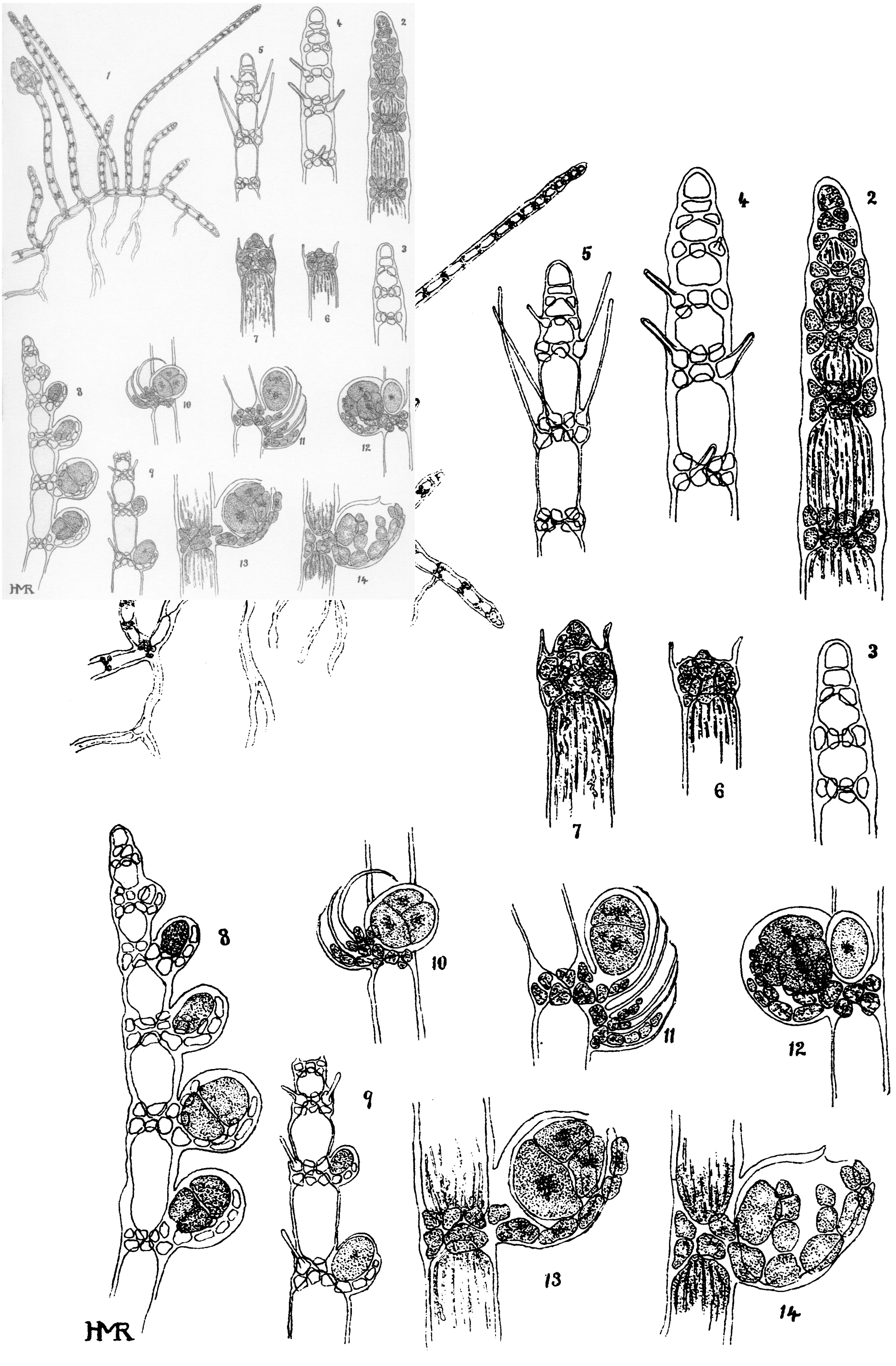
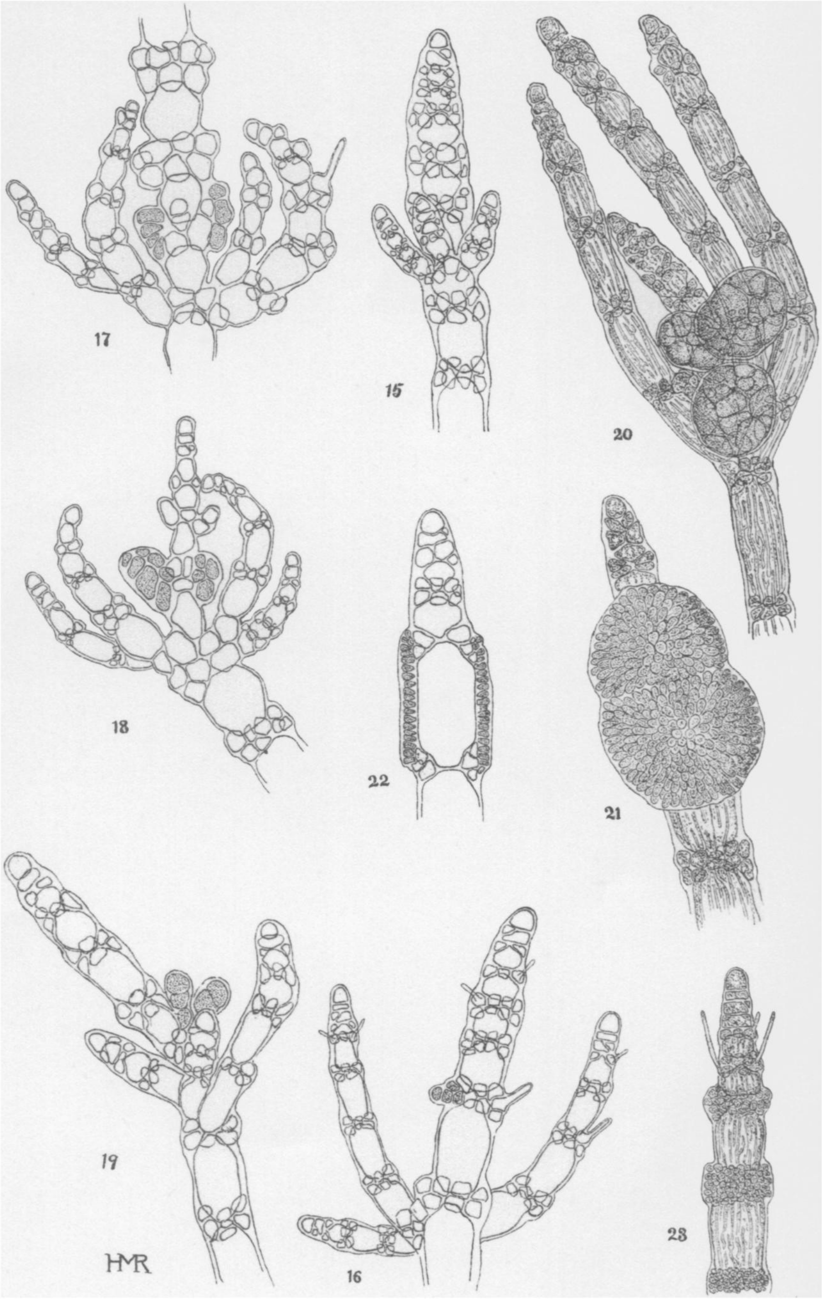
PL. 21.



CERAMOTHAMNION CODII



CERAMOTHAMNION CODII

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Ceramothamnion codii, a new Rhodophyceous Alga

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(WITH PLATES 21, 22)

While in Bermuda during February, 1898, the writer collected a quantity of *Codium tomentosum* which proved on examination to have growing upon it an epiphytic rhodophyceous alga that is decidedly peculiar in character. More material was obtained during the February of the following year and from these collections the following account of the morphology of this alga was written. *Codium tomentosum* is common enough in the waters about the islands, but only that obtained at two localities on the south shore proved to have growing upon it this *Callithamnion*-like alga. *Codium* is a favorite abiding place of many small algae and it is very common to find the fronds fringed with small species of *Callithamnion*, *Ceramium*, *Ectocarpus*, *Goniotrichum*, etc. The form, however, which is the subject of this paper is not so conspicuous, scarcely more than slightly reddening the parts on which it grows, the filaments being so short and so fine as to be scarcely visible to the naked eye. Only occasionally are small tufts found in the dichotomies of its host and even these would be hardly noticed were it not for their red color.

In habit it suggests a form like *Rhodochorton Rothii*, there being a prostrate filament which sends up at irregular intervals erect filaments, that are always unbranched except under certain

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conditions of fruiting. Since this plant lives upon the soft tissues of another alga there are also developed well-marked rhizoids which penetrate between the external cells of the *Codium* (Fig. 1).

The prostrate and upright filaments are alike in structure, differing only in the somewhat larger size of the former, which measure from 30–50 μ in diameter at the internodes, while the latter vary from about 20–35 μ. The structure of the filaments is peculiar, and at once attracts attention, from its similarity yet unlikeness to that of two other genera of algae. They are monosiphonous as to the elongated internodal cells (which average 50 μ long), while at the nodes there are rows of small cells. Such a condition suggests at once *Ceramium* but the general appearance of the cells is far more like those of *Callithamnion* (Fig. 2). The wall is somewhat thick and the sides parallel, never bulging as in *Ceramium*, while the chromatophore is very distinct and made up of thickened strands as is usual in *Callithamnion*. In consequence of this the internodes are distinctly red in color, never, as is often the case in *Ceramium*, quite diaphanous, and it may be added the tips of the young branches are straight, never circinate. The nodal cells, which in the oldest part of the frond are in from three to four rows, lie closely packed between the adjoining internodes. They do not ever, even in the oldest portions of the plant, proliferate downwards and upwards to form a cortication, but only overlap the somewhat tapering ends of the internodal cells, lying in the constrictions formed between the latter, so that they do not produce any marked nodal swellings. Their chromatophores are of the same appearance as those of the internodes, but the granulation of the contents is more marked and consequently it is of a deeper color. One might describe the general appearance of the filament as that of *Callithamnion* and its allies with the addition of nodal cells.

At the tips of the filaments are found small apical cells, from which the formation of nodes and internodes takes place in an entirely regular manner (Figs. 2, 3). There is first cut off from the apical cell by a transverse basal wall a single indifferent cell. This indifferent cell soon divides from its upper end, by four obliquely anti-clinal walls of small cells which when seen in optical section are naturally triangular ; the hypothenuse being the newlyformed wall. These are the young nodal cells and their formation does not appear to be always simultaneous, nor when successive, in any particular order. The next step in the formation of the node is the rounding off of these cells and their transverse division. There are now two rows of cells, which subsequently may become by division two double rows of eight cells each, or sixteen cells in all at the nodes. Sometimes but one of the original two rows divides again transversely, in which case there will be but twelve cells in the node, disposed in one single and one double row. But in the older parts of the filaments the rows ultimately become displaced, owing to irregular divisions of some of the cells.

The internodal cells develop by enlargement in all directions, particularly in length, and the original tapering end caused by the obliquely formed walls of the nodal cells increases rather than diminishes. It is this constriction between the internodes which is, as has before been said, closely packed with the nodal cells, the outline of the filament being almost straight and continuous. The erect branches arise from the nodes of the procumbent filaments, one of the nodal cells on the upper surface taking on the function of the apical cell of the branch. Each node may produce its branch, but no cases were observed where more than one arose from a single node (Fig. 1). The rhizoids which grow into the tissue of the *Codium* also originate from nodal cells of the main filament, but from the under side of course, and make their way downwards into the tissue of the host. They are colorless, or almost so, and often sparingly dichotomous, exhibiting no especial peculiarities. Branching of the upright filaments is seen only in connection with the formation of certain forms of the fruit which will be considered later.

Some of the material collected was found to be provided with hairs which arise from the nodal cells. While usually short (Fig. 4) they are sometimes prolonged as in Fig. 5. The short hairs cannot be considered simply younger ones for they are often found on fully matured portions of the filament. Their contents indicate that they are simply sterile hairs, as it is very scanty and gathers at the end in the way common among such organs. They were also found on material in all conditions of fructification.

The fact that they must be regarded as merely sterile is of importance in another consideration to be taken up later. While the bulk of the material examined was quite destitute of them it is barely possible, although not at all probable, that this condition was brought about by the shedding of the hairs, since indications were seen of their abstriction in certain cases.

While the structure of the frond of this alga is not without interest the fruit, at least the tetraspore, is more especially noteworthy. Indeed as regards certain features in the growth of the tetraspores the writer has found no mention of a similar condition among other Florideae. As would be supposed the tetraspores are formed at the nodes in the younger portions of the upright branches ; one can easily observe almost all stages on a single filament (Fig. 8). The tetrasporangium itself always arises from a cell in the upper of the two rows of cells at a young node, only a single one developing at one node. After a slight enlargement, chiefly elongation, of this mother cell of the tetraspores the adjoining nodal cells are seen to become actively concerned in the growth (Fig. 8). They begin to grow outwards and around the young tetrasporangium forming bract-like enveloping branches, something like a stichidium with but a single group of tetraspores. The extent to which the enveloping branches develop varies, sometimes only one is produced (Fig. 13), representing the prolongation of a single row of nodal cells, sometimes the single row itself branches and forms an almost complete covering to the tetrasporangium, while again several separate rows of nodal cells may develop in this fashion. The tetraspores are not tetrahedral, but are arranged rather in the cruciate fashion, where however the longitudinal divisions following the first transverse division of the mother cell, are in planes at right angles to each other. When the filaments lie in the position which they naturally assume when attached to the basal prostrate filament, it appears that it is always the distal or upper cell in the young tetrasporangium which has divided in a plane at right angles to the field of vision (Figs. 10, 12, 13). After the spores are ripe the outer wall of the sporangium, which is often considerably thickened, breaks open at the apex and they escape, leaving the empty shell attached to the plant. Then follows a peculiar proliferation, if one may term it so, of the cell which lies at the base of the tetrasporangium. From this a new tetrasporangium starts up, growing into the cavity of the old one and provided with its own thickened wall. This is in turn replaced by another, and yet another, so that one often finds a young tetrasporangium surrounded by the remains of the walls of perhaps four or five earlier ones (Figs. 10, 11), something in the manner of the proliferation often noticed in the zoösporangia of *Saprolegnia.* In no instance was more than a single ripe tetrasporangium observed at each node; in the case shown in Fig. 12, the new one has begun its development somewhat earlier than is usual, but no doubt had the older tetraspores been discharged it would have been forced into the empty cavity. This condition of the successive formation of new tetrasporangia within the older ones does not seem to have been noted in any other form, a fact which makes the appearance presented by this alga in its tetrasporic stage very characteristic.

The antheridia, which like the antheridia of the bulk of the Florideae, consist of an aggregation of small cells each containing a single spermatium, originate from the outgrowth of the nodal cells. The latter, dividing into many small cells, spread upwards and downwards from the nodes, usually completely covering the intervening internodal cells (Fig. 22); sometimes considerable portions of a filament are so modified to form one long antheridium, or, to speak more strictly, a collection of the unicellular antheridia. The spermatium-bearing cells may remain closely appressed to the sides of the internodal cell as is shown in the section in Fig. 22, or, by reason of a growth more rapid than the lengthening of the internodes, may bulge outwards in more or less rounded masses (Fig. 21). The antheridia were never seen on the same plants as the tetraspores, but usually occur alone, although in a few cases they were observed on the same plant or even the same filament as certain polyspores.

These polyspores which first attracted attention in their mature condition naturally aroused the suspicion that they might be favellae of the *Callithamnion* type, especially since the well-defined antheridia described above were also seen. But as the following description shows the most careful search failed to substantiate any such idea, although the development of these spores were worked out in detail. Unfortunately nothing which could be called a trichogyne or trichophoric apparatus was revealed. The polyspores occur as considerable aggregations, enclosed in a definite wall, and borne in the axils of certain specially developed branches (Fig. 20). It is only in this connection that the upright filaments ever branch ; an irregular whorl of branches is formed with the main axis of the filament continuing above them, and at their bases are formed one or more large favella-like masses of irregularly arranged spores. The branches, which vary from two to as many as five in number, usually assume ultimately an equal length with the original axis, sometimes even surpassing it in importance and in so doing often push it to one side, making it quite indistinguishable. In consequence of this the masses of mature polyspore often appear to be borne terminally on an irregularly forked filament. By following their development it can be seen, however, that these branches arise as lateral outgrowths from the cells of the younger nodes (Figs. 15, 16, 17), originating in all respects after the manner in which the upright filaments spring from the prostrate one, except that two or more arise from each node. After the beginning of these outgrowths it appears that the axis from which they spring ceases to develop to any extent, all of its vitality being spent in the production of the polyspores and the accompanying whorl of branches. In a few instances a second node below also produces a few side branches, but these never develop to any great length, nor were polyspores seen to be borne in their axils. In the formation of a branch one of the nodal cells takes on the function of an apical cell while the surrounding ones multiply somewhat and as the new internodal cell formed from the apical cell enlarges from around its base a junction with the parent axils, four or five nodes, and occasionally many more are formed before any activity in the direction of the origin of the polyspores is to be observed. For this reason it is often difficult to trace the exact point of origin of the latter. The polyspores, however, were found to originate always from the node of the main axis immediately above the one which gave rise to the whorl of branches (Figs. 16, 17, 18). The cells begin to multiply more rapidly, and form groups of four or five cells ; these ultimately by still further division and by great increase in size produce the favella-like masses figured in Fig. 20. First one group develops, then another closely following, and perhaps even a third and fourth mass of spores is formed, reminding one of the polyspores found in certain species of *Ptilota*. In the older stages it is impossible to tell where the spores are attached, they are often so displaced as to appear to have to do with the next node below the one from which they really arose, although in following their development no case —with the possible exception of the one shown in Fig. 17—was observed where any other than the first node above the whorl of secondary branches produced any outgrowth. Signs of a slight activity in the nodes above were occasionally noted, but this never led to the formation of polyspores.

The masses of polyspores, apparently mature, vary in size from about 50–80 μ by 35–60 μ, they are never spherical, and vary also in the number of spores contained, which was from twelve to twenty, in specimens counted. The spores themselves are also irregular in shape and size being, irregularly polyhedral from compression, and measuring from 15 to 20 μ in their greatest diameter.

In connection with the development of these apparently wholly non-sexual spores, it is necessary to refer again to the hair-like processes found springing from the cells in some instances. As has been previously noted, some of the material collected showed the hairs while other material was devoid of them. When first observed on a polysporic specimen it was hoped that they were, indeed, trichogynes, but subsequent investigation showed that these hairs also occurred on antheridial and even tetrasporic specimens (Figs. 9 and 23), and that their lack of contents except at the very tip placed them undoubtedly in the category of the hair-like processes common with other algae. Nor was anything in the nature of trichophoric apparatus found in connection with them. Even where they were present on the same node with the young polyspores (Fig. 16) there was no connection apparent. In short, they lacked the easily recognized appearance of trichogynes and trichophoric cells, which is familiar to any one who has studied Florideae.

To sum up, it may be said that this alga, epiphytic on *Codium tomentosum*, is in habit similar to *Rhodochorton*, and in the general appearance of the cell and its chromatophore like other forms of the genus *Callithamnion;* that it has, as to the filament as a whole, the structure of a *Ceramium* with its clustered nodal and bare internodal cells, and that it is furnished with polyspores reminiscent of those of *Ptilota*. The general appearance, however, is very dissimilar to any of these, and it is further marked by the peculiarity of the proliferating tetrasporangia. Since it is, therefore, impossible to place this form satisfactorily in any of the established genera, and since its peculiarities are sufficiently marked, it seems justifiable to assign it to a new genus, the diagnosis of which is appended.

Ceramothamnion gen. nov.

Plant consisting of prostrate filaments giving rise above to erect filaments, and below to rhizoids. Erect and prostrate filaments same in structure, monosiphonous throughout with small cells collected at nodes : growing tip straight, never circinate : chromatophores rhodophyceous, in elongated bands running almost the length of the internodal cells : tetraspores, antheridia and polyspores present : tetrasporangia borne at nodes : cruciate ; provided with enveloping sterile cells, proliferating by successive formation of new tetrasporangia inside of the old.

Ceramothamnion codii sp. nov.

Prostrate filaments 30–50 μ in diam., never branched except for erect filaments which arise at nodes : erect filaments 20–35 μ in diam., from 0.5 to 1.5 mm. long, sterile, always unbranched, branches arising in connection with polyspores ; outer wall usually unbroken and continuous, but at times pierced by sterile hairs which arise from the nodal cells ; nodal cells in maturity usually 12–16 at each node, never forming a complete cortication to the internodal cells ; mature tetrasporangia single at node, 30–45 × 20–30 μ, partially covered with enveloping sterile cells : proliferating as described above : polysporangia variable in size, 35–60 × 50–80 μ arise laterally from the erect filaments, and consist at maturity of clusters of from 10 to 20 polyspores : several of the clusters—from two to four—are grouped together and are surrounded by protecting branches. Procarpes and cystocarps not observed. Antheridia in masses sheathing the internodal cells, or forming more or less rounded masses from node to node. Polyspores and antheridia usually on separate plants, occasionally on same filament.

Habitat.—Forms minute tufts or small expanses on *Codium tomentosum* among the cortical ramifications of which its rhizoids penetrate. Collected in February on the south shore of the main island of Bermuda.

Explanation of Plates 21, 22

PLATE 21

FIG. 1. Habit, showing the prostrate and erect filaments, rhizoids and masses of polyspores.

FIG. 2. Growing tip, showing also the appearance of the chromatophores in the internodal cells.

FIG. 3. Same in different stage of division.

FIG. 4. Tip provided with short hairs.

FIG. 5. Tip where the hairs are greatly elongated.

FIGS. 6 and 7. Formation of new apical cells in a broken filament.

FIG. 8. Tetrasporangia in various stages of development.

FIG. 9. Tetrasporangia on same filament with hairs.

FIGS. 10 and 11. Tetrasporangia developing within the empty walls of previous ones.

FIG. 12. Tetraspores almost ripe with young tetrasporangium developing.

FIG. 13. Fully developed tetrasporangium showing bract-like covering.

FIG. 14. Empty sporangium after discharge of spores.

PLATE 22

FIG. 15. Showing the origin of whorl of secondary branches.

FIGS. 16, 17, 18. Various stages in development of polyspores.

FIG. 19. Abnormal development of polyspores at an early stage.

FIG. 20. Mature polyspores.

FIG. 21. Mature antheridium.

FIG. 22. Optical section of antheridium.

FIG. 23. Young antheridia developing. The nodal cells above have produced hairs.

All the figures were drawn with an Abbe camera. 1, × 30 diam.; 2–14, × 420 diam.; 15–23, × 480 diam., and reduced about one third. The drawings were made from specimens preserved in alcohol and treated with lactic acid causing the outer wall to swell away from the contents to some extent.